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The variants of *Ravenala* in natural and anthropogenic habitats

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Introduction

The hitherto monospecific *Ravenala madagascariensis* (the traveler's palm, Strelitziaceae) has recently proved to be a complex aggregate of at least four variants, which may later deserve the rank of species. These variants can be distinguished according to macromorphological characters, growth habits and habitat preferences (Blanc *et al*., 1999; Hladik *et al*., 2000). Our subsequent investigations have resulted in the discovery of the natural habitats of these four recognized forms, which are presented in this chapter. A comparison of the adaptive responses of these various forms to the habitat disturbance, resulting mainly from the human impact, are also presented here.

Growth habits and morphological diversity of the *Ravenala*

The major characteristics of the growth habits and other distinctive characters of the four recognized forms of *Ravenala* (for further details see Blanc *et al*., 1999) are the following:

(1) The first form (*malama*) is the most strikingly divergent variant, especially with respect to its juvenile phases. The leaves of the young plant, before reaching about 1.5 m in length, are spirally arranged, instead of being fan-shaped (the classical aspect of most *Ravenala*). This young plant looks like an *Asplenium nidus* (Aspleniaceae, fern) fallen to the ground from its epiphytic habitat. The torus arrangement of the *malama* leaves is secondarily acquired through a precocious torsion of the leaf stalk, which is very short in this form (Fig. 1). Such a torus arrangement reflects an adaptation to the low light intensity of the forest understory (Blanc, 1992). The distribution of the leaves around a vertical symmetry axis prevents the blades from overlapping; furthermore, the parabolic shaping of each leaf blade also results in efficient capture of diffuse low light.

At older stages, the morphology and arrangement of the leaves is progressively modified: the leaves become arranged in one plane, like the frame of a fan, in relation to the original distichous initiation, without secondary orientation, and the length of the petiole progressively increases. In a full grown *malama* the overlapping of the leaves, arranged as a fan, reduces light absorption, especially when the level of the canopy is reached by this typically shade-adapted forest form.

(2) The second form (*hiranirana*) presents, during its first stages of growth, the usual pattern of most *Ravenala,* in that the leaf blades have long petioles and are arranged in a plane (fan-shaped). However, in contrast with *malama*, the older individuals of the *hiranirana* form present a slight and regularly alternate shift of the leaf blades. This shift allows an efficient orientation of the leaf blades to light, useful when the plant is growing towards the forest canopy, reflecting a higher light request than for the first form.

(3) The third form (*bemavo*) is adapted to the intense light conditions of open areas. During all its life stages, the leaves of *bemavo* show a perfect fan arrangement. This form is also the most resistant to water stress, as the overlapping of the leaf blades might reduce transpiration and photoinhibition of photosynthesis.

(4) The fourth form (*horonorona*), also has a perfect fan leaf arrangement during all its life stages, but it has a smaller stature. It is mainly characterized by its cespitose habit, with new stems arising at the base of the older ones. This form is potentially immortal, as each new shoot develops its own system of adventitious roots.

All these forms have contractile roots, a crucial adaptation to several habitats. The contractile roots allow the stem apex to sink into the soil. This pattern of growth and establishment is responsible for the increase of the stem diameter through the initiation of numerous roots along the buried stem base. As a result, the individuals that grow on unstable or inundated soils are stabilized, as well as those on steep slopes. Similarly, in the young stages of any form, the stem apex is protected against the fires, either of anthropogenic origin or natural, that occur frequently in the savanna-like slopes of eastern Madagascar.

The growth rate of these various forms of *Ravenala* can be estimated from our field observations. For instance, in June 2000, most individuals of the four forms presented new emerging inflorescences on each side of the leafy crown, usually in the axil of the fourth to eighth leaf from top. Usually, two inflorescences appear on each side of the crown. These four inflorescences are consecutive or separated by one sterile leaf. The annual flowering is followed by vegetative growth during which 3 to 5 leaves are produced on each side of the fan. Thus each *Ravenala* produces about 8 leaves without an inflorescence, plus 2 to 4 leaves supporting inflorescences, per year. This regular alternate positioning of sterile and flowering phases is shown by the scars left by old infructescences along the stipe, at intervals of 60 to 70 cm, the mean annual increase in height of most individuals.

From an evolutionary viewpoint, we have suggested (Blanc *et al*., 1999) that the suckering habit and the perfect fan-shaped leaf arrangement correspond to a primitive condition. This would imply that *Ravenala* first inhabited more or less inundated lowland forests, with a form corresponding to the present *horonorona*. Afterwards, a form such as *bemavo* could have invaded the steep slopes covered by open forests. Finally, forms such as *hiranirana* and *malama* would have colonized closed forests, the *Malama* being the most morphogically divergent and the best adapted to the conditions of the understory.

The first results obtained by analyzing the ITS (Internal Transcribed Spacers) sequences of the DNA of individuals of the four forms of *Ravenala* (Robert, 2000) are in agreement with such an evolutionary scenario. The form *horonorona* appears as the most primitive, while *hiranirana* and *bemavo* are weakly separated (as shown by a cluster analysis), and *malama* does appear as the most evolved form.

The natural habitats of the *Ravenala* forms

The different forms and populations of *Ravenala* described here have been observed in the eastern part of Madagascar, mainly on the slopes originally covered by lowland eastern and mid-altitude forests, between 0 and 1,000 m elevation.

It is generally difficult to define with certainty the natural habitat of any plant species. This is especially true in places such as the steep slopes of the eastern forest of Madagascar, where the impact of human activities and cyclones are particularly intense. The same type of difficulty also arises with the origin of vegetation growing in low swampy areas, since artificial excavations, quite common along the roads, become filled with water and associated plants.

The *malama* form

This form (called *fontsy malama* in the Bezanozano area) grows in undisturbed forests, mostly between 600 and 1,100 m. It is particularly abundant around Andasibe, and in the Parc National de Ranomafana. In contrast to the other forms, *malama* is clearly adapted to the microclimate of the forest floor in the understory of undisturbed rainforests. The seeds germinate in this shady environment and the seedlings grow among typical herbaceous and shrubby understory species, such as member of the Urticaceae, Balsaminaceae, Piperaceae, Pandanaceae, Myrsinaceae. The young stages of *malama*, with their secondary spiral leaf arrangement, are perfectly adapted to these shady environments (Fig. 1). The older stages grow through the mid-layer stories, and the crown finally reaches about 15 m in height, the leaves expanding their blades in the forest sub-canopy levels, although some of the oldest individuals emerge above the forest canopy.

The *hiranirana* form

The second forest form (called *fontsy hiranirana* in the Bezanozano area), is common in mid-elevation forests, although rare above 900m. In contrast to *malama*, it can also be found at low altitude. It germinates and establishes mainly in medium-size forest gaps —and the frequent occurrence of cyclones favors such gaps. The peculiar fan-shaped leaf arrangement of the young stages of this form is adapted to light intensity of these forest gaps, higher than in the understory. The adult crown reaches about 15 m, and the leaves usually are exposed to the sun at canopy level. The rapid growth allows this form to reach the canopy before complete closure of the gap. In disturbed forested areas, between 600 and 900 m, the *hiranirana* is the most common form of Ravenala. It can be found mixed with the *malama* form at the transitional zone between lowland and mid-elevation forest. At lower elevations, it occurs together with the third form (*bemavo*), usually in the forests growing on steep slopes.

The *bemavo* form

It is not easy to define the natural environment of *bemavo* (as it is called in a portion of the Betsimisaraka area), since this form is the most common one, found growing in diverse anthropogenic situations. It is found up to 1,000 m, but is most common between 200 to 600 m, which corresponds to the eastern elevational zone that is most heavily deforested. It never occurs inside the rainforest, except on steep ridges on well drained thin substrates, where it is exposed to high levels of light. This is the tallest form, reaching 20 to 25 m in height.

The natural environment of the *bemavo* appears to be the low forest covering the steep slopes

of the inselbergs between 300 and 500 m, such as those around Ifanadiana, along the road to Mananjary (Fig. 2). These inselbergs are the exposed portions of Precambrian basement rocks, which are metamorphic and igneous in origin, and include mostly crystalline rocks such as granite and migmatites (Du Puy & Moat 1996). The almost vertical and often bare parts of these inselbergs have patches of classic saxicolous plants, such as *Kalanchoe* (Crassulaceae), *Aloe* (Asphodelaceae), and *Xerophyta* (Velloziaceae). On more moderate slopes (between 30° and 60°), the typical low forest can grow on a thin substrate. These forests usually reach less than 10 m in height, with a floristic composition including forest trees such as *Dilobeia* and *Tambourissa* species, as well as small trees or shrubs (i.e. *Phyllarthron* and *Phylloxylon*). In these dry conditions, the delicate herbaceous plants such as *Gravesia* (Melastomataceae), *Impatiens* (Balsaminaceae), or *Elatostema* (Urticaceae) species are absent. The *bemavo* is the only abundant form of Ravenala in this forest type, although some *hiranirana* may appear where more water retentive soil allows some higher trees to grow.

The *bemavo* germinates on thin soil, usually in small crevices situated between large boulders. Due to the low height of trees and the presence of large boulders devoid of vegetation, the light is more intense than in the understory of a tall forest, and the sunflecks are more abundant. The roots of *bemavo* are usually superficial, imbricated in a thick layer covering the rocks. Due to mechanical instability of the substrate, older *bemavo* trees frequently fall but, in many instances, the apical part still grows, forming a sharp angle with the horizontal stem. It appears that *bemavo* is clearly a form adapted to high light intensity and dry conditions, and this is probably why it is so successful on deforested slopes.

The *horonorono* form

The fourth form called *horonorona* (after its name in a part of the Betsimisaraka area) occurs mainly at low altitude (below 300 m). It is morphologically characterized by a tufted, or cespitose habit. This form is clearly the most hygrophilous one. The natural habitats appear to include two types of environments. First, it is found in hilly landscape where some deep stream valleys escape seasonal fires and still contain natural vegetation (Fig. 3). In such gullies, the slopes just above the stream are covered with *horonorona*. Above this zone, *horonorona* becomes less abundant, with fewer stipes. A completely developed *horonorona* includes 6 to 8 stipes, reaching about 10 m in height, with several younger offsets. In this undisturbed environment, the offsets originate at ground level in the moist soil, as well as at 50 cm to 1 m above the ground. The gullies are thus covered by a low forest canopy almost exclusively constituted by the *horonorona* crowns. In the understory of this habitat grow some other hygrophilous plants, such as Cyperaceae, Pandanaceae, and Taccaceae. The *horonorona*, although not growing in the streambed, is obviously adapted to a very humid environment.

The second type of natural *horonorona* environment corresponds to the flat lowland peat swamps, which are common above the sandy substrate along the coast. Besides the *Sphagnum* species, the local plant community includes *Utricularia* (Lentibulariaceae), *Burmannia* (Burmanniaceae), *Drosera* (Droseraceae) and *Eriocaulon* (Eriocaulaceae) together with some *Pandanus* (Pandanaceae) species, mostly *P. platyphyllus*. In this habitat, where the water depth is usually less than 10 cm, *horonorona* is usually less than 5 m tall, with a tuft reduced to one main stem on some offsets. Seeds can germinate either on the wet soil, or just below the water surface. Some young or weakly developed *horonorona* also occur at the edges of he coastal forest growing on sandy substrate. No other forms of the *Ravenala* are present in all these types of habitat.

The *Ravenala* forms in disturbed habitats

Most of the present-day visitors of Madagascar believe that the traveler's tree is exclusively located on the deforested slopes of the eastern part of the island, particularly below 600 m where *Ravenala* are so abundant that the vegetation has been often described under the term of "ravenala forest". In such zones, the *bemavo* and *horonorono* forms are the most common. However, the typical forest forms, *malama* and *hiranirana,* may also persist in disturbed forests.

The *malama* form may occur outside the forest, but only when the climatic conditions are sufficiently humid. It may be observed in *savoka* (abandoned areas of cleared forest after planting of agricultural crops), at around 1,000 m elevation, near Andasibe, that is in perhumid environmental conditions. Even in such conditions, the *malama* cannot germinate and establish in completely open areas, since the young seedlings observed in these disturbed areas are located in the shade of trees and shrubs forming the first stages of a secondary forest. Once the apex is buried in the soil by the contractile roots, the *malama* saplings can withstand the subsequent clearing of the vegetation, although they appear to be quite weak, with their leaves partially destroyed by excessive light. In these open mid-elevation areas, the *malama* usually remains at the early stages of development, without an emerging stipe.

The *malama* can also be found in forest remnants above 600 m, where it is often mixed with *hiranarana*, although this other form is mostly located on edges and open gaps. In contrast, at such sites in the larger forest fragments (greater than 1 ha) the *malama* grows among the oldest trees. Some young or weakly developed *malama* have also been observed in Eucalyptus plantations near Andasibe.

The *hiranirana*, which is also originally a forest form, appears to be quite ubiquitous. It can grow from near sea level to 1,000 m and it is always associated with large shrubs and/or trees, but not necessarily large forest remnants. In these types of disturbed forests such as the Station Forestière d'Andasibe, seed dispersal and successful establishment of seedlings occur mainly within a radius of about 50 m around the parent tree. In contrast to *malama*, the *hiranirana* can germinate and develop in open areas, surrounded by larger plants. At the forest edges, often at the ecotone with *savoka*, a nearly continuous line of hiranirana can often be found, seemingly forming an efficient barrier against fire. Even when the leaves are burnt, the stipe of *hiranirana* and its apex remain alive.

Due to its original edaphically xeric environment, the *bemavo* form is the most successful on the very steep slopes where the practice of slash-and-burn cultivation has opened up the landscape (Rasolofoharinoro et al. 1997; Razafy Fara et al. 1997). In these areas (Fig. 4), the *bemavo* could be either tended, or planted, since it provides leaves for house roofing and flattened pieces of the stipe for floors and walls. It is also used as an ornamental species in gardens. At its earliest stage, when the apex is not yet buried in the ground, *bemavo* saplings can be destroyed by fire. Later, the apex, which is protected inside the soil, increases in size, as do the emerging leaves. When the leafy crown reaches about 4 m in height, the apex emerges from the ground and may be destroyed by savanna fires. This vulnerability persists for 2 to 3 years, until the stipe is about 1.2 m. At this point, the *bemavo* can withstand subsequent fires and persist in areas of slash-and-burn cultivation.

In Madagascar, high densities of *bemavo* are beneficial, not only for provision of building materials, but also because the apex of young plants is consumed by people. The *bemavo* may also play an important role in forest regeneration, given that its stipe height and high densities can provide protective shade for a considerable number of forest tree and shrub species (Robert, 2000).

Below 200-300 m elevation, the *horonorona* is the most common form of traveler's tree, found on

coastal hills, where human density is extremely high. This hygrophilous form appears as being very sensitive to the slope inclination and resulting water drainage, as well as to frequency of fires, both being factors at the origin of water stress. In such ecological situations, the tuft is generally reduced to an aboveground stipe, plus one to five underground stems that produce reduced leaves (a large total leaf area should not be compatible with water stress). Domestic animals may also regularly graze on new leaves produced by these underground stems.

Along deforested riverbanks, at low altitude, the *horonorono* can form an almost continuous line of less than 10 m in height. Similarly, it can be present in man-made excavations along roads. After being filled with water, these excavations are colonized by *Typhonodorum* (Araceae), *Pandanus* species (Pandanaceae) and Cyperaceae. However, as *Ravenala* seeds sink in water, the seedlings cannot establish where the water is deeper than 5-10 cm.

Past and future research on the *Ravenala* forms

The large variation in the environmental conditions faced by the traveler's trees, and the possible occurrence of ecotypes have been referred to in previous works, although usually not clearly described (Koechlin *et al*., 1974; Dumetz, 1988; Andrianifahanana, 1992). Research on floral biology and pollination, carried out either in Madagascar (Kress *et al*., 1994; Birkinshaw & Colquhoun, 1998), or in countries where *Ravenala* is an alien species (Calley *et al*., 1993) have demonstrated that experimental self-pollination may produce some seeds; however, cross pollination is the common rule in wild conditions. Lemurs, when licking nectar at the base of the huge inflorescences may contribute to cross-pollination by carrying pollen on their fur.

Further research is needed to address issues of cross-fertilization of different Ravenala forms in sympatry (Blanc *et al*., 1999). Are there barriers favoring self-pollination or an apomictic system? Future research, that include molecular approaches, will be necessary to complete the pioneering studies of Smith *et al*. (1993) and Kress (1995) and to understand the ecology of the various forms of *Ravenala*.

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Figures & legend

Fig. 1 - Secondary spiral leaf arrangement in a young malama in the Parc National de Ranomafana forest understory.

Fig. 2 – A natural bemavo population in the low forest covering an inselberg near Ifanadiana.

Fig. 3 - Gullies covered with a dense natural horonorona population, near Brickaville.

Fig. 4 - The perfect fan leaf arrangement of *bemavo* in an open area near Beforona.